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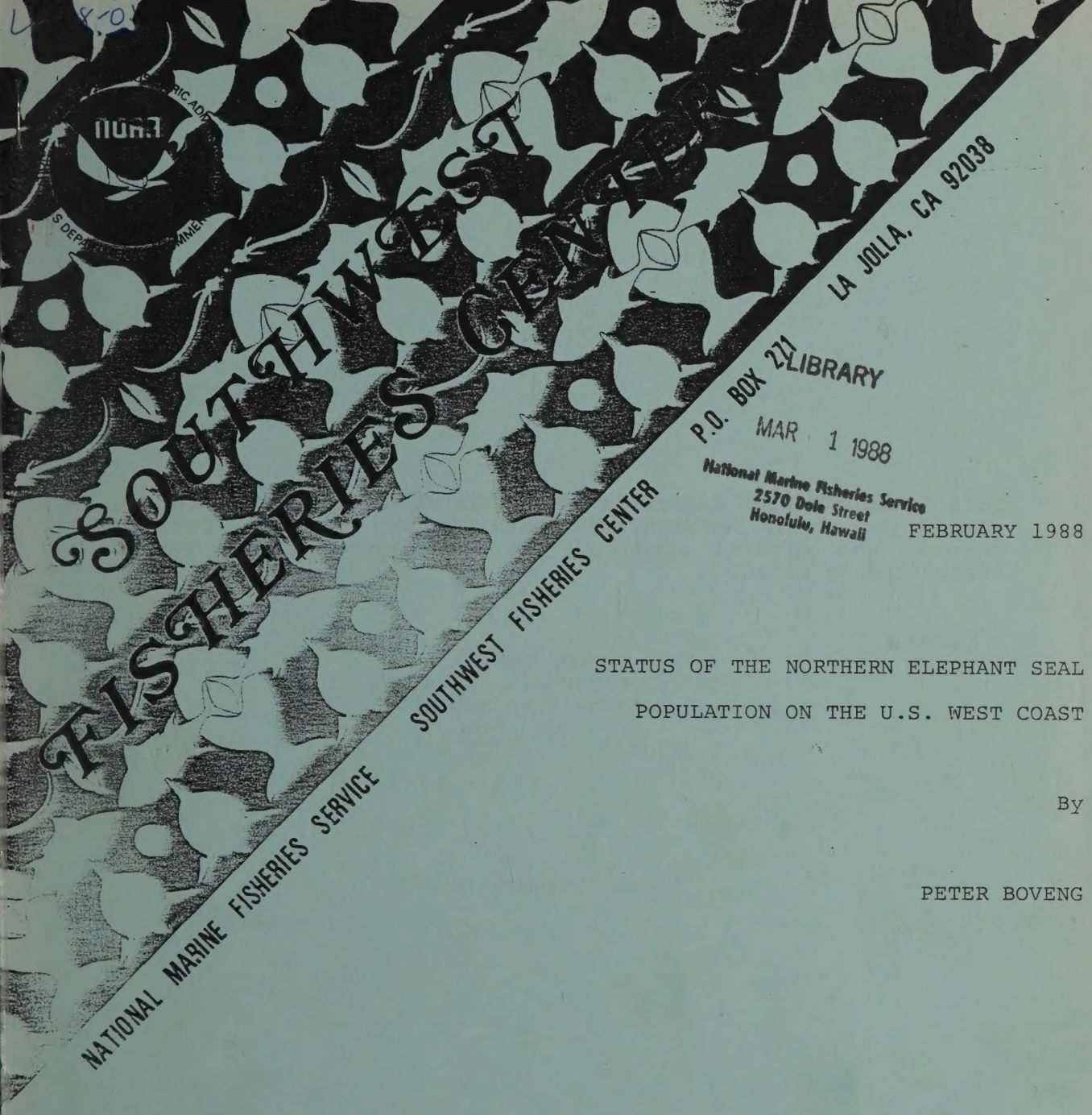

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STATUS OF THE NORTHERN ELEPHANT SEAL POPULATION ON THE U.S. WEST COAST

By

PETER BOVENG

ADMINISTRATIVE REPORT LJ-88-05

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STATUS OF THE NORTHERN ELEPHANT SEAL POPULATION ON THE U. S. WEST COAST

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5 February 1988

ADMINISTRATIVE REPORT LJ-88-05

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INTRODUCTION

The northern elephant seal (Mirounga angustirostris) is one of several species of pinnipeds which inhabit the Pacific coast of the United States. Management and conservation of elephant seals are subject to the guidelines and regulations of the Marine Mammal Protection Act of 1972 (MMPA) and subsequent amendments to the Act. Management under the MMPA is premised on determinations about whether the population is in a condition that can be considered optimum (for the animals and the ecosystem) and whether a proposed level of take is detrimental. Consequently, the status of the population must be assessed periodically. This document is a synthesis of the currently available information on the status of the elephant seal population of the U. S. west coast.

History of Exploitation and Management

The exploitation and subsequent recovery of the northern elephant seal population has been described in several papers (e.g., Bartholomew and Hubbs 1952, Bartholomew and Hubbs 1960, LeBoeuf and Panken 1977, LeBoeuf and Mate 1978, Stewart et al., in press). The seals were harvested extensively for oil in the late 19th century. Bartholomew and Hubbs (1960) speculated that the entire species was comprised of fewer than 100 individuals at the turn of the century. The Mexican government afforded protection to the species in 1922 (Bartholomew and Hubbs 1960), and the U. S. followed suit a few years later (Le Boeuf and Panken 1977). Steady population growth evidenced by colonization of new rookeries and increasing size of existing rookeries, has continued to the present. The potential for interactions with fisheries and other human uses of the marine ecosystem presumably has increased with the size of the population.

Basis for Management (the Marine Mammal Protection Act)

The MMPA recognizes marine mammals as components of the marine ecosystem. Noting also that some species or stocks of marine mammals have already been endangered by man's activities, the MMPA requires maintenance of stocks above levels at which they would lose their function in the ecosystem. Although ecosystem function forms the basis of the primary objective of the MMPA, marine mammal management in practice is directed toward maintaining optimum sustainable population sizes, a second major objective of the Act.

The working definition of "optimum sustainable population" (OSP) is a range of population size between the environmental equilibrium (carrying capacity, or K) and the level from which maximum productivity would result. The lower limit of the range of OSP is the maximum net productivity level (MNPL). Implicit in the

notion of OSP is the recognition of the instability of population levels below MNPL; that stocks which are reduced to levels below MNPL may decline precipitously, even when subject to apparently moderate perturbations in the environment or the harvest (Clark 1976, Beddington and May 1977). On the other hand, populations at levels above MNPL should be more resilient to variable environments and harvests. Population dynamics theory predicts that populations above MNPL will tend to equilibrate with a harvest, provided that the harvest is not at a rate greater than the maximum at which the population is capable of growing (Beddington and May 1977).

The net production of the population at the MNPL is the theoretical upper limit to a rate of harvest or incidental take which could be consistent with maintenance of a population within the range of OSP. A level of take (replacement yield), spread proportionally over all age and sex classes, which would cause a population to equilibrate between MNPL and the carrying capacity, is necessarily lower than the rate of maximum net production (MNP).

The present assessment of the northern elephant seal population uses abundance data, considered with information about incidental mortality, to estimate the current size of the population, to estimate the current replacement yield, and to estimate the status of the population relative to the OSP.

METHODS OF STOCK ASSESSMENT

OSP Determination

Two basic approaches have been used for determining the status of marine mammal populations relative to the OSP. One approach requires direct estimation of the the population sizes which define the range that is considered to be the OSP (i.e., determining the values of MNPL and K). This method has been used for dolphins in the eastern tropical Pacific tuna fishery (Smith 1983) and for harbor porpoise on the U. S. west coast (Barlow 1987). In both of those assessments, the method used to estimate K was a back-projection from current abundance levels to the pre-exploitation level (K), using estimates of the annual take (Smith and Polachek 1979). Using this method, the OSP determination is relative to the maximum population level that the environment could support at the beginning of the exploitation period (K is an estimate of "historic K"). This method is not applicable to elephant seals because the pre-exploitation abundance is unknown and cannot be estimated due to the lack of quantitative information about the nineteenth century harvests which reduced the population to near extinction.

The other approach to stock assessment depends on inference from some index which varies in a predictable fashion with population status (e.g., growth rates or other vital rates, physical growth rate or condition, parameters such as age at sexual maturity or age at first reproduction). Then the value of the index is used to determine qualitatively whether the population is depleted or in the range of OSP, without actually determining the population sizes which define the range. This approach makes an OSP determination that is relative to the current condition of the environment. Dynamic response analysis (Goodman, in press), which was previously applied to California sea lions (DeMaster et al. 1982) and to elephant seals (Boveng et al. in press), is a form of this method which uses density dependent changes in the population growth rate (indexed by changes in pup counts) to infer the qualitative status relative to MNPL. Two forms of the dynamic response method are used in the present assessment. The first is an extension of the analysis in Boveng et al. (in press) to include more recent census information. The second form uses the pup counts to estimate the per-capita production curve from which a qualitative status determination is made in the manner proposed by Goodman (in press).

Estimation of Rates of Increase and Replacement Yields

Rate of change in population size can be estimated directly from trajectories of a population index or census through time, or indirectly from estimates of survival and reproduction rates. The former method is an estimate of the actual population growth rate which occurred on the chosen time interval. In the absence of information about actual trends in population size, the latter method can be useful for determining the range of growth rates which would be expected on the basis of observed or assumed life history parameters of the species. This range may then be compared to estimated or proposed rates of take to predict the degree of impact on the stock. In the present case, trends in pup counts are assumed to be at least as reliable as elephant seal life history data. Therefore, the sections entitled POPULATION GROWTH RATES and REPLACEMENT YIELD are based on analysis of trends in pup counts.

STOCKS OF ANIMALS INVOLVED

The MMPA defines a "population stock" or "stock" as a group of the same species or smaller taxon in a common spatial arrangement, that interbreed when mature. Thus, the distinction between a population and a stock is not clear in the MMPA. In this assessment, I use the term "population" loosely, with no

particular implication of demographic discreteness. I use the term "stock" more specifically, as defined in the Act.

In addition to the ambiguous terminology in the Act, for some species of marine mammals the stock definition is difficult to apply or may not be sufficiently rigorous (Barlow 1987). However, the evidence cited below is sufficient to apply the definition to northern elephant seals.

The entire population of northern elephant seals may have descended from a small group of animals located on Isla de Guadalupe, Mexico around the turn of the century (Townsend 1899, Bartholomew and Hubbs 1960). The recovery of breeding colonies on California islands and recently documented movements of tagged seals (Condit and Le Boeuf 1984, Stewart et al. 1985, Huber et al. 1986) indicate that there is currently interbreeding between the colonies. The interchange may result from young animals which begin breeding at colonies other than their birthsites (Cooper and Stewart 1983, Condit and Le Boeuf 1984). Elephant seals are usually site tenacious after onset of sexual maturity (Le Boeuf et al. 1972). Condit and Le Boeuf (1984), in a discussion of sightings away from rookeries, suggested that the northward expansion of the recovering population may have been facilitated by non-breeding season migrations to northern feeding areas.

The current breeding range of the species is between 27°50'N and about 41°45'N latitude (Bonnell et al. 1983) but very little breeding takes place north of the Farallon Islands (37°41'N). Several seals born (and tagged) in central and Southern California have been resighted in British Columbia and sightings of untagged adult and sub-adult males are common there during the summer (Condit and LeBoeuf 1984). Rare sightings of elephant seals have been reported from as far north as Alaska (Willett 1943, Antonelis and Fiscus 1980, Condit and Le Boeuf 1984) and as far west as the Hawaiian Islands (Antonelis and Fiscus 1980, Condit and LeBoeuf 1984).

Based on the studies of movements, breeding, and population biology cited above, I have assumed that the northern elephant seals which breed on U. S. coasts comprise a single stock as defined in the MMPA. By that definition, the elephant seals breeding on Mexican rookeries (e.g., Bartholomew and Hubbs 1952, Rice et al. 1965, Le Boeuf et al. 1975, Le Boeuf and Bonnell 1980) should probably be included in the same stock. However, because the data available from Mexican populations are insufficient to conduct an assessment, I have not included them.

ESTIMATION OF CURRENT POPULATION SIZE

The life history of northern elephant seals precludes a complete census of the population. The animals ashore at any

particular time represent only a portion of the total population. The spread in pupping dates ensures that by the time numbers of adult females ashore have peaked, some females will have already departed. The only age class which lends itself to a nearly complete census is the cohort of pups born during January and February. Thus, the majority of the useful census information comes in the form of pup counts.

Figure 1 shows the trajectory of total counts of pups at San Miguel Island (Odell 1971, Le Boeuf 1977, Mate 1977, Le Boeuf and Bonnell 1980, Antonelis et al. 1981, Bonnell et al. 1980, Cooper and Stewart 1983, Stewart et al. in press), San Nicolas Island (Odell 1971, Odell 1974, Antonelis et al. 1981, Le Boeuf 1977, Le Boeuf and Bonnell 1980, Stewart and Yochem 1984, Stewart et al. in press), Año Nuevo Island and Año Nuevo Point (Orr and Poulter 1965, Rice et al. 1965, Le Boeuf and Briggs 1977, Le Boeuf and Bonnell 1980, Reiter et al. 1981, Le Boeuf and Panken 1977, Le Boeuf and Condit 1983, Le Boeuf[1], Parsons[2]), and Southeast Farallon Island (Huber et al. 1986, Huber[3]). Pup counts were available for all colonies from each of the years shown in Figure 1 except Año Nuevo Island counts for the years 1982, 1984, and 1985. Therefore, a pup count of 900 was assumed for Año Nuevo Island in those years (the mean pup count for 1981, 1983 and 1986 was 919). An error in this assumption of even several hundred pups would have little effect on the shape of the curve in Figure 1.

The total number of pups counted in 1986 at the rookeries described in the previous paragraph was 14,332. For all rookeries but San Miguel Island, the 1986 counts included dead pups and thus are estimates of the numbers of pups born. Pup mortality at San Miguel Island between 1979 and 1982 ranged from 3 to 8 percent (Cooper and Stewart 1983). Estimates, from aerial photographs, of pup mortality at San Miguel Island in 1985 and 1986 were less than 5 percent[4]. For the purpose of estimating total population size,

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[1]Personal communication. B. J. Le Boeuf, University of California, Santa Cruz.

[2]Personal communication. R. Parsons, California Department of Parks and Recreation.

[3]Personal communication. H. Huber, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Seattle, Washington.

[4]Personal Communication. W. Perryman, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California.

I used the pup count as an estimate of births without correcting for mortality at San Miguel. In addition, roughly 100 pups have been born annually in recent years at smaller rookeries including Point Reyes (19, Allen 1987), Santa Rosa Island (2, Stewart and Yochem 1986), Santa Barbara Island (57, Lowry et al. 1987), San Clemente Island (1, Oliver[5]), Cape San Martin (20, Brownell[6]), and Point St. George (1 to 6, Bonnell et al. 1983). Adding approximately 100 pups from these smaller rookeries to the counts from the major rookeries, the total number of births in 1986 was estimated to be 14,432.

I estimated the total population size by constructing hypothetical schedules of survivorship separately for males and females and then, assuming a stable age distribution, computing the predicted age structure for a population growing at the recently observed (see POPULATION GROWTH RATES) rate of 8.75 percent annually. The assumed survivorship schedules were derived from those given by McCann (1985) for southern elephant seals (Mirounga leonina). The southern elephant seal survivorship schedules were fitted[7] to non-linear, 5-parameter functions to facilitate an analysis of the sensitivity of the population estimate to variation in survival rates (presented below). The resulting survivorship schedules, and predicted age structures for males and females are shown in Table 1. The corresponding estimate of population size is 3.69 times the number of female pups plus 3.36 times the number of male pups. Sex ratio at birth was assumed to be unity. Therefore, the total U. S. elephant seal population size was estimated to be 50,800 just after pups were born in 1986. If the population grew at the recently observed rate of 8.75 percent, the estimated population size would be about 55,000 in 1987 and 60,000 in 1988.

Stewart (1980) estimated that the total elephant seal population size just after the pupping season was 3.6 times the number of pups born. His estimate assumed that all mature females bear a pup, that breeding age males are .3 times as numerous as

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[5]Personal communication. C. Oliver, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California.

[6]Personal communication. R. Brownell, Jr., U. S. Fish and Wildlife Service, San Simeon, California.

[7]Barlow, J. and P. Boveng. Modeling mortality for marine mammal populations. Unpublished manuscript. National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California.

mature females, and that the number of immatures (excluding pups) is equal to the number of matures. Le Boeuf and Bonnell (1980) used a factor of about 4 to convert from counts of pups born to total population size. Thus, several independent estimates put the total population size at approximately 3.5 to 4 times the pup count.

To investigate the sensitivity of the population estimate to assumptions about survival rates, the survivorship curves were scaled[7] by various values of longevity (defined here as the 99th percentile of the age distribution). Scaling by a smaller value for longevity is equivalent to decreasing the survival rate at each age. Conversely, larger longevity values imply higher survival rates. For each value of longevity, the resulting population estimate was computed as described above. Figure 2 shows contours of population size estimates obtained by allowing longevity of males and females to range between 9 and 19 years. The solid square in Figure 2 represents the population estimate (50,800) resulting from the longevities (16 years for females, 14 years for males) obtained from the southern elephant seal survivorship curves (McCann 1985). Combinations of extreme values for longevity of both sexes result in population estimates ranging from about 37,500 to 58,000 seals.

Females elephant seals known to be older than 9 years of age have commonly been observed at Año Nuevo Island (Reiter et al. 1981) and the Farallon Islands (Huber et al. 1986). Of the male seals present during the 1984 and 1985 breeding seasons at the Farallons (Huber et al. 1986), over 20% were classified as bulls (8+ years old). Thus, longevity of 9 years for both sexes is almost certainly too low. To the extent that the other assumptions hold, the lower limit of the population estimate for 1986 would be greater than 37,500. Available data are not sufficient for a similar assessment of the reliabilty of the upper estimate of 58,000 seals.

Le Boeuf and Bonnell (1980) estimated that there were about 60,000 northern elephant seals in 1977, about 25,000 of which were associated with U. S. rookeries. Applying a growth rate of 8.75 percent per year (see POPULATION GROWTH RATES), to their estimate would result in a 1986 U. S. population of about 53,000 which is similar to the estimate I derived above. The limited data available for estimation of population size and growth rate on Mexican rookeries suggest that recent growth has been slower than for the U. S. population (Cooper and Stewart 1983). Using a minimum estimate of 35,000 for Mexican rookeries (Le Boeuf and Bonnell 1980), and an estimate of 50,000 for U. S. rookeries, the present total northern elephant seal population probably numbers at least 85,000.

POPULATION GROWTH RATES

Cooper and Stewart (1983) found that populations at California rookeries, as indexed by pup counts, were growing at rates ranging from 13.6 to 53.3 percent per year, with an average of about 14.5 percent per year. They also estimated that the Mexican population (from which California rookeries were receiving immigrants) grew at about 8.3 percent annually between 1965 and 1977. The rate of growth of the total California breeding population during recent years is estimated below.

From a regression of the natural logarithm of the pup count on year of the count, the average rate of growth in total California pup counts was 13.7 percent annually between 1965 and 1986 (slope=.128, s.e.=.0034, $P<<.001$, $R^2=.992$). Because the pup counts for the years 1980 through 1986 appear to follow a different slope than the earlier counts (Fig. 3), separate regressions were computed for the years 1964 through 1978 and for 1980 through 1986. The estimated rate of growth for the former period was 14.2 percent annually (slope=.133, s.e.=.002, $P<<.001$, $R^2=.999$). The estimated rate of growth for only the years 1980 through 1986 was 8.75 percent annually (slope=.084, s.e.=.007, $P<.001$, $R^2=.963$), which is significantly different from the former slope ($P<.001$).

Berkson and DeMaster (1985) used a model to investigate the reliability of pup counts for estimating discrete rates of change in population size. They found that the rate of change in pup counts may be a biased estimator of total population change and that the direction of the bias depends on the relative timing of density dependent pup survival and the census. When the primary density dependent process in their model was adult survival, the bias was small. Elephant seal pup mortality between birth and weaning may be density dependent (Reiter et al. 1981, Huber et al. 1983), but the effect has not been demonstrated on the largest rookeries (San Miguel and San Nicolas). Also, the probability of a pregnant female hauling out to pup on a particular rookery may be density dependent (Reiter et al. 1981). Thus, for a particular rookery there may be density dependent processes both preceeding and following the census of pups born. However, the extent to which these density dependent processes are regulating the total pup count is not known well enough to predict the magnitude or direction of bias in the estimated growth rate.

INCIDENTAL MORTALITY

In a previous assessment of elephant seal population status (NMFS 1980), incidental mortality in commercial fishing operations was considered to be rare, although the need for more accurate data was cited. Recent observations by California Department of

Fish and Game (CDFG) continue to support the view that incidental take of elephant seals is low in California fisheries. However, because most concern has been for other species of pinnipeds, there is still not much quantitative data available to accurately assess elephant seal mortality.

Miller et al. (1983), in a survey of several California fisheries during 1979 and 1980, estimated that about 25 elephant seals were killed each year, all by entanglement in southern California gill nets. This estimate was projected from the observed number of mortalities using the ratio of observed to total fishing effort, but no confidence limits were available.

In north-central California fisheries, CDFG observers recorded 4 elephant seals taken in 1985 (Wild 1986) and 2 elephant seals taken in 1984 (Wild 1985). For comparison, 58 harbor seals and 11 California sea lions were observed taken in the same studies. All 6 elephant seal mortalities were in nets set for halibut in the Half Moon Bay area (Mussel Rock to Pigeon Point). No elephant seal mortalities were observed in the Bodega Bay (Russian River to Pt. Reyes) or the San Francisco area (Pt. Reyes to Mussel Rock).

Bishop (1985) reported no elephant seal mortalities in 10 months (Nov. 1983 - Aug. 1984) of observations of coastal set-net boats between Pt. Piedras Blancas and the Santa Maria River. There were 277 net-pulls observed which was roughly 10 percent of the total fishing effort in that area. In southern California nearshore gill and trammel net observations, there were no observed elephant seal mortalities in 1983, 1984, or 1985 (Collins et al. 1984, Collins et al. 1985, Collins et al. 1986).

Diamond et al. (1986a) reported 2 elephant seals caught (both in the same net) during observations of the 1983 shark/swordfish drift gill net fishery. There were 71 net pulls observed, representing less than 1 percent of the total fishing effort. In the same period of observation, 6 California sea lions were killed (2 of those were in the same net as the 2 elephant seals), which was projected to a total kill of about 900 (s.e. = 425) sea lions. The elephant seal mortality was not projected to a total kill. There were nc elephant seal mortalities observed in 44 net pulls (<1% of total effort) in the same fishery during 1984 (Diamond et al. 1986b). In 1985, 2 elephant seals were caught in 66 observed pulls (again, <1% of total effort) (Diamond et al. 1987).

There is apparently some incidental mortality in offshore trawl and longline fisheries. Condit and Le Boeuf (1984) found reports of 9 elephant seals caught in fishing gear off the coasts of California, Oregon and Washington. However, the animals seem to be widely dispersed at sea because offshore sightings are usually of solitary animals (Antonelis and Fiscus 1980). Therefore, mortality in pelagic fisheries is probably rare.

Stewart and Yochem (1987) documented the frequency of entangled and scarred elephant seals in surveys of San Miguel and San Nicolas Islands between 1983 and 1986. Approximately .15% of elephant seals observed in 1983 and 1984 were entangled and an additional .09% had scars, possibly caused by previous entanglement. In 1985 and 1986, about .16% were entangled and .20% scarred. They observed that those apparently low rates of entanglement had not had obvious effects on the elephant seal population trend. However, they noted a greater tendency for juveniles to be entangled and therefore, they cautioned that for populations which are monitored by numbers of births, detection of entanglement effects may be delayed until the affected age classes are recruited.

In summary, the limited data available suggest that elephant seal mortality incidental to fisheries is low. Only a few have been observed taken in California gillnet fisheries. The tendency for these animals to feed in deeper, offshore waters (Le Boeuf et al. 1985, Le Boeuf et al. 1986) probably minimizes their contact with other coastal gillnet type fisheries in Washington and Oregon. For the same reasons, contact with pelagic fisheries seems to be rare.

OSP DETERMINATION

In this section, two forms of the dynamic response technique are used to assess the status of the elephant seal stock relative to its optimum sustainable population (OSP) level. Both methods assume that the level of mortality due to incidental take is negligible.

Dynamic Response Analysis

1) Pup count trajectory

Boveng et al. (in press) applied the dynamic response method to trajectories of pup counts through 1982 at Southeast Farallon, San Nicolas, and San Miguel Islands, and through 1980 at Año Nuevo Island. The method used in that study is described briefly here before presenting results based on pup counts through 1986.

When the mechanism of density dependence, the accuracy of the censuses and the amount of environmental variation are unknown (see Gerrodette, in press), a decision rule is needed to arrive at a compromise between using many censuses (the assessment will not be current) and using only a few recent censuses (the assessment may be influenced by noise in the data). In the technique presented in Boveng et al. (in press), curvature produced by noise in the trajectory is "filtered" out by increasing the number of censuses until the results are consistent with the expected results from a trajectory which has curvature due only to density

dependence. This is accomplished by fitting second degree polynomials to intervals of the pup count trajectory. For a given interval size (number of censuses), repeatedly shifting the location of the interval by one pup count and computing a new regression produces a series of second order regression coefficients. The shape of the curve generated by plotting each coefficient against the mean time of the cenuses in the corresponding interval is examined for inconsistency with the shape predicted from density dependence considerations. The predicted shape is shown in Figure 4 which was generated by applying the method to the well known logistic growth curve. Census intervals which are too short will reveal curvature due to noise rather than density dependent changes in growth rate. The resulting plots of second order coefficients will cross the zero line more than once, or in the wrong direction.

Figure 5 shows the results of applying the moving interval method to the curve of total pup counts in Figure 1. The quadratic regressions computed on intervals of 5 or 6 censuses produce second order coefficients which alternate between positive and negative values, thus failing the requirement that the curve of second order coefficients cross zero only once, from positive to negative. Increasing the number of censuses to 7 results in a curve which is not inconsistent with the shapes in Figure 4, at least to the extent that within statistical error, the curve begins above the zero line, then intercepts the zero line but does not return to significantly positive values. The curves resulting from 8 or more censuses per interval are even more like the curves in Figure 4. No census interval size results in curves with significantly negative coefficients that are consistent in shape with the expected form (Fig. 4).

The second order regression coefficient from the regression on the 7 most recent total pup counts (1980-1986) is -35.5 with an estimated standard error of 52.9. Therefore, although the coefficient is negative, it is not significantly different from zero (at a significance level of .05). This result is taken to indicate a population near its MNPL (Goodman, in press; Gerrodette, in press; Boveng et al., in press). This status determination should be associated with the midpoint of the census interval (1983) rather than the most recent endpoint (1986).

In Boveng et al. (in press) there was not a large enough sample of years during which the 4 major U. S. island rookeries had been counted to do the analysis on the total pup count. However, in separate analyses of the 4 rookeries, Boveng et al. (in press) found that the pup counts through 1982 indicated that all 4 colonies were still below their respective MNPL's (but those assessments were actually attributed to dates at the midpoints of intervals of censuses, several years prior to 1982). The present finding, that the stock has apparently reached its MNPL suggests

that a significant change in the status has occurred in the intervening years.

The form of the dynamic response method applied here, namely that of analyzing the shape of the trajectory of pup counts, may be less sensitive to errors such as random measurement errors but more sensitive to real environmental perturbation than the general form which operates on the per-capita production curve (Goodman, in press). This is because estimation of production as the first difference of the abundance time series is sensitive to random noise but will tend to remove serial correlation caused by an environmental perturbation. The recent El Niño event was a major environmental perturbation for many species (Barber and Chavez 1983, Stewart et al. in press). The dynamic response analysis applied above cannot distinguish between a true density dependent reduction in population growth rate and the effect of correlated deviations from the expected growth curve which would result from a short term contraction in the carrying capacity. Therefore, a second dynamic response analysis, utilizing the more general form, was also applied to the elephant seal data.

2) Per-capita production curve

The general form of the dynamic response method, as proposed by Goodman (in press), is based on local analysis of the slope of the relationship between per-capita production and stock size, evaluated at current stock size. Per-capita production in year i (P_i) has been estimated here as the first difference in pup counts ($N_{i+1} - N_i$), divided by N_i. To the extent that pup counts represent total stock size, this estimate of production is unbiased (Goodman, in press). For any count which was not followed by a count in the subsequent year, the first difference was estimated by interpolating between the count and the next actual count, assuming that growth was exponential in the intervening years. The relationship between the resulting estimates of per-capita production and stock size is shown in Figure 6.

The choice of a model for fitting the per-capita production curve is not a simple one. One of the merits of the dynamic response method is that because the analysis of the shape of the production curve is purely local the model need not have a mechanistic or population theoretical basis, provided the model adequately describes the shape for the range of stock size of most concern (what comprises an adequate fit is an issue in itself). Some mechanistic models would put constraints on the location of the MNPL, making the dynamic response analysis less general. However, I have used a mechanistically based model for the per-capita production curve for the following reason: For a particular set of points such as those displayed in Figure 6, there is a very large number of ad hoc models (e.g., polynomial functions of stock size), any one of which might fit about as well

as any other. Limiting the scope of possibilities to those which have a basis in population dynamics theory greatly simplifies the choice. Provided that a sufficiently general model is chosen, no real constraints are placed on the location of the MNPL.

The data in Figure 6 were fit to a generalized logistic model (Gilpin and Ayala 1973, Gilpin et al. 1976, Pomerantz et al. 1980) for the relationship between per-capita production and stock size:

$$P = r\{1 - (N/K)^z\}. \qquad [1]$$

This model allows for the population production curve to be asymmetric, depending on the value of the parameter z. If z is equal to 1, the model is simply the familiar logistic equation. Values of z greater than 1 result in population production curves with peaks shifted to the right, which have been related on theoretical grounds to life histories typical of marine mammals (Eberhardt and Siniff 1977, Fowler 1981). Because there is no known form of this model, except for special cases (e.g., z=1 or z=2), which explicitly describes the time trajectory of stock size, the per-capita production form was retained, and analyzed by the dynamic response method.

Assessing the status of the population relative to its MNPL requires estimating the slope of the tangent line to the per-capita production curve at N^*, the stock size of interest (Goodman, in press). For the model presented above, the first derivative with respect to stock size (N) is

$$dP/dN = -zrN^{z-1}/K^z. \qquad [2]$$

The slope, α, of the tangent line is obtained by evaluating the right hand side of this derivative at N^*. The slope and the observed per-capita production associated with N^* define a straight line which intercepts the production axis at some value, say β. As shown by Goodman (in press), if $N^* > -\beta/2\alpha$, the stock size N^* is above MNPL, if $N^* = -\beta/2\alpha$ then N^* is equal to the MNPL, and if $N^* < -\beta/2\alpha$, N^* is below MNPL. Equivalently, because this model describes a particular MNPL for any set of parameter values, N^* could simply be compared to the estimated MNPL.

Estimation of the three model parameters r, K, and z, from the elephant seal per-capita production estimates was accomplished by a non-linear least squares regression using Marquardt's algorithm. To estimate the parameter variances and covariances, the non-linear regressions were repeated in a jackknife fashion, each time eliminating one of the data points and computing the parameter estimates based on the remainder. The variances of this set of "jackknifed" regression estimates were used as the parameter variance estimates. The estimated parameter values for

the full complement of data points, as well as for each jackknife estimate are shown in Table 2.

The 1985 data point was highly influential, as indicated by the relatively large value of K which resulted from excluding it (Table 2). Also, the three large values of z, which correspond to per-capita production curves that are flat for a broad range of stock size and then rapidly decline to zero, resulted from including the 1985 point. Observation of Figure 6 suggests that the 1985 point is not in character with the other production estimates. Futhermore, because there is some reason to expect that the low (actually negative) production estimate for 1985 (Fig. 6) may have resulted from an environmental perturbation (poor recruitment of cohorts born or conceived during the El Niño) (Stewart et al. in press), the analysis was repeated, excluding the 1985 estimate.

The parameter estimates and standard deviations from the jackknife regressions without 1985 (Table 3) were: r = .149 (s.d. = .004), K = 20,244 (s.d. = 3,633), and z = 2.19 (s.d. = .50). The per-capita production curve represented by the model with those parameter values is shown in Figure 7. Following equation [2] above, the quantity $-\beta/2\alpha$ computed from the estimated 1986 stock size (N^*) equals 12,391. Because the 1986 stock size estimate of 14,332 is greater than 12,391, the conclusion is that the 1986 stock size estimate represents a population above its MNPL. (As noted by Goodman (in press), the value of 12,391 is not itself an estimate of the MNPL, unless it is equal to the stock size N^* from which it was obtained).

From a statistical standpoint, the procedure of choosing a nonlinear model over a simpler linear one is not justifiable unless the ability of the nonlinear model to describe the data is significantly better than the ability of the linear model or there is compelling evidence that the underlying model is genuinely nonlinear. A linear relationship between per-capita production and stock size defines a logistic growth curve for which the MNPL is equal to K/2. When the per-capita production estimates (excluding 1985) are subjected to jackknife linear regression, the resulting parameter estimates are: r = .160 (s.d. = .005) and K = 34,902 (s.d. = 4948). These parameters produced the straight line in Figure 7. In this case, $-\beta/2\alpha$ is equal to K/2, or 17,451 pups and the 1986 estimate of 14,332 would be slightly below MNPL. The nonlinear model explains slightly more of the variance in the data (27 percent) than the linear model (24 percent), but neither model accounts for a statistically significant fraction of the variance (P=.34 for nonlinear model, P=.20 for linear model). Because the underlying model for elephant seals is presumably nonlinear with a value of z greater than 1 (Eberhardt and Siniff 1977, Fowler 1981), I have retained it as the more appropriate model.

Immigration from Mexican elephant seal colonies (e.g. Cooper and Stewart 1983) may have had a profound effect on the estimates of per-capita production, particularly estimates for the earliest years (Fig. 6). Because the form of density dependent response of the immigration rate is unknown, I assumed that immigration and natural production respond to the same carrying capacity and that the processes combine to form a smoothly unimodal population production curve.

3) Summary of Dynamic Response Analyses

Analysis of the shape of the pup count trajectory suggests that the population is near, or perhaps just past its MNPL. Local analysis of the per-capita production curve, also estimated from pup counts, indicates that the population is past MNPL if a nonlinear (i.e., theta-logistic of Gilpin and Ayala (1973)) model is used, or that the population is slightly below MNPL if a linear logistic model is used. As Gerrodette (in press) showed, the region immediately surrounding MNPL is the region in which dynamic response analysis is least accurate in predicting the direction of departure from the MNPL. Thus, although the elephant seal stock is apparently near its MNPL, whether it is actually above or below that point cannot be determined from the pup count data alone.

If there is actually a significant rate of incidental mortality, not accounted for in the dynamic response analysis, the true population status could be different than that revealed by the analysis. In particular, if incidental mortality has been increasing, true status would be lower, relative to the MNPL, than the apparent status.

The influence of immigration from Mexican elephant seal colonies on the per-capita production relationship needs further study. Specifically, tagging studies such as those reported in Le Boeuf *et al*. (1974) and Le Boeuf *et al*. (1975) should be undertaken cooperatively by U. S. and Mexican researchers with the objective of determining rates of exchange based on effort corrected tag and resight data.

Other Information Bearing on Status

Recent observations of new elephant seal breeding sites (e.g., Le Boeuf and Panken 1977, Bonnell *et al*. 1983, Allen *et al*. 1987, Stewart and Yochem 1986), particularly those on mainland beaches, have inspired speculation that the current population size may be greater than the historic (pre-commercial-exploitation) levels. One hypothesis assumes that mainland breeding was limited by large terrestrial predators and aboriginal human hunters (Le Boeuf and Panken 1977). Also, Stewart *et al*. (in press) reviewed archeological studies which showed that frequency of pinniped remains found in Channel Island Indian

kitchen middens decreased in the more recent layers, leading them to speculate that over-exploitation may have occurred and that elephant seals may currently be more abundant than they ever were in human history. If these hypotheses are true, and if the results of the dynamic response analysis discussed above are correct, then not only the present carrying capacity but the present MNPL might be larger than the size of the population when non-native people began exploitation in the early 19th century.

Condit and Le Boeuf (1983) observed that elephant seal pup mortality at Año Nuevo Island increased with the density of the breeding colony. Density dependent changes in reproductive parameters, such as age at first reproduction or age specific fecundity, have not been demonstrated (but may eventually be observed at intensively studied colonies e.g., Huber 1987). Although such density dependent relationships could presumably be used to infer population status (see review by Fowler (1987)), there is not enough known about elephant seal life history to determine the types of changes that would indicate whether a population was above or below its MNPL.

REPLACEMENT YIELD

As discussed in the section on POPULATION GROWTH RATES, the rate of increase in counts of pups born on U. S. rookeries between 1980 and 1986 was in excess of 8 percent per year. Assuming that the rate of increase in pup counts is representative of the current rate of increase in stock size, the current replacement yield is estimated as the product of the growth rate and the stock size. Thus, a current growth rate of 8.75% and a 1986 stock size of 50,800 results in an estimated replacement yield of about 4,450 animals. In other words, the estimate suggests that the 1986 stock level could sustain a take of about 4,450 animals (but the take would have to be distributed in proportion to the current age and sex structure). If the stock has continued to grow at the observed rate of increase in the pup counts, the estimated 1988 replacement yield would be about 5,250 seals.

The decline of the pup count in 1986 suggests that the current rate of increase may not be as high as the average rate for the past 7 years. Therefore, the replacement yield estimated above should be considered a maximum estimate. Also, Barlow (1987) suggested expressing replacement yields and maximum allowable take estimates in terms of percent of stock size because numerical quotas can have a destabilizing effect. Expressed on that basis the current replacement yield estimate is simply equal to the estimate of the growth rate, 8.75 percent.

SUMMARY: STATUS OF THE STOCK

Data from references indicate that there were about 14,400 northern elephant seal pups born on U. S. rookeries in 1986. The corresponding total population size was estimated to be about 50;800 animals. The apparent growth rate since 1980 has been about 8.75 percent annually, but because the number of pups born actually decreased in 1986, the current growth rate may be smaller.

Incidental mortality of this species in U. S. fisheries seems to be low. On that assumption, the status of the stock relative to its OSP was determined using a dynamic response method for non-harvested stocks. The result of that analysis indicated that the elephant seal stock is currently near its MNPL (the lower limit of the range called OSP), but the direction of departure cannot accurately be predicted. If the assumption regarding the insignificance of the harvest were not true, particularly if incidental mortality has been increasing, the true population status would be lower (relative to the MNPL) than indicated by the dynamic response analysis. Other data, such as current versus historic breeding range and density dependent life history observations were insufficient for quantitative assessment of status. However, because of the possibility that pre-historic abundance of elephant seals was limited by human hunters and large predators (LeBoeuf and Panken 1977, Stewart *et al.* in press), present abundance may be even greater than it was when white men settled in California (Stewart *et al.* in press).

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Table 1. The survivorship schedules used for estimating northern elephant seal population size (l_x, FITTED) were obtained by fitting a 5-parameter nonlinear function to the southern elephant seal survivorship schedules (l_x, SES) presented by McCann (1985). The predicted stable age distribution[a] (C_x) was computed for a population growing by the observed recent annual factor of increase, $\lambda = 1.0875$.

Age (x)	FEMALES				MALES			
	SES	FITTED			SES	FITTED		
	l_x	l_x	$\lambda^{-x}l_x$	C_x	l_x	l_x	$\lambda^{-x}l_x$	C_x
1	1.000	1.000	.920	.271	1.000	1.000	.920	.298
2	.600	.600	.507	.150	.600	.715	.605	.196
3	.510	.510	.397	.117	.510	.541	.421	.136
4	.449	.449	.321	.095	.422	.424	.303	.098
5	.395	.396	.260	.077	.350	.341	.224	.073
6	.348	.350	.212	.062	.290	.278	.168	.054
7	.306	.308	.171	.051	.241	.228	.127	.041
8	.269	.271	.139	.041	.193	.188	.096	.031
9	.237	.238	.112	.033	.145	.153	.072	.023
10	.209	.208	.090	.027	.101	.124	.054	.017
11	.184	.180	.072	.021	.071	.097	.039	.012
12	.162	.154	.056	.017	.050	.073	.027	.009
13	.136	.129	.043	.013	.035	.050	.017	.005
14	.106	.106	.033	.010	.024	.030	.009	.003
15	.079	.083	.024	.007	.017	.015	.004	.001
16	.055	.061	.016	.005	.012	.005	.001	.000
17	.036	.040	.010	.003				
18	.022	.023	.005	.001				
19	.011	.010	.002	.001				
20	.004	.003	.001	.000				
TOTALS			3.389	1.000			3.086	1.000

[a]The stable age distribution, $C_x = \dfrac{\lambda^{-x}l_x}{\sum_{y=1}^{\infty} \lambda^{-y}l_y}$

Table 2. Parameter estimates for non-linear least squares regression of per-capita production estimates using the model: $P=r\{1-(N/K)^z\}$. Parameter values are shown for the full data set and for individual "jackknife replicates", each of which results from excluding one point.

Excluded Point	Parameter Estimates r	K	z
none	.1418	14591.34	5.9185
1964	.1390	14552.95	6.6558
1968	.1466	14656.39	5.0632
1972	.1357	14510.77	7.9574
1976	.1529	14700.08	4.4818
1977	.1269	14487.04	14.7488
1978	.1256	14490.61	15.6301
1980	.1445	14522.44	6.8855
1981	.1411	14534.93	6.9001
1982	.1397	14486.29	14.3224
1983	.1476	14729.38	3.5484
1984	.1464	14302.12	4.4656
1985	.1491	20244.23	2.1655

Table 3. Parameter estimates for non-linear least squares regression of per-capita production estimates using the model: $P=r\{1-(N/K)^z\}$. Parameter values are shown for the full data set (excluding 1985) and for individual "jackknife replicates", each of which results from excluding one point in addition to 1985.

Excluded Point	Parameter Estimates r	K	z
none	.1491	20244.23	2.1655
1964	.1487	20195.59	2.1858
1968	.1578	21280.93	1.7649
1972	.1466	20176.21	2.2599
1976	.1563	18588.21	2.3700
1977	.1454	25149.46	1.6033
1978	.1496	30701.85	1.1692
1980	.1490	18431.62	2.8330
1981	.1490	20215.58	2.1767
1982	.1469	20148.14	2.8719
1983	.1505	18234.91	2.1619
1984	.1487	17326.95	2.6861

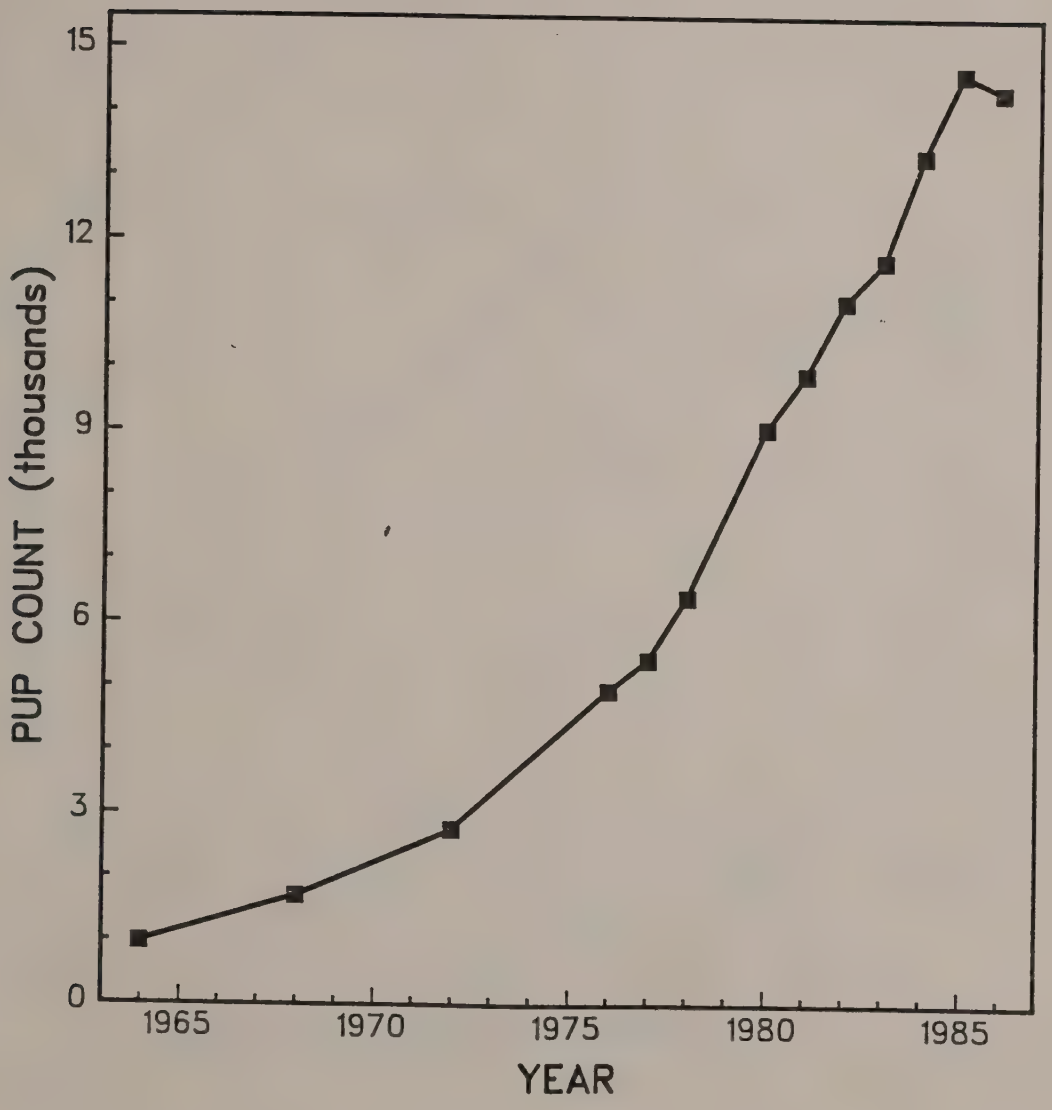

Figure 1. Total numbers of northern elephant seal pups counted at San Miguel Island, San Nicolas Island, Año Nuevo Island, Año Point, and Southeast Farallon Island. Sources of counts are cited in the text.

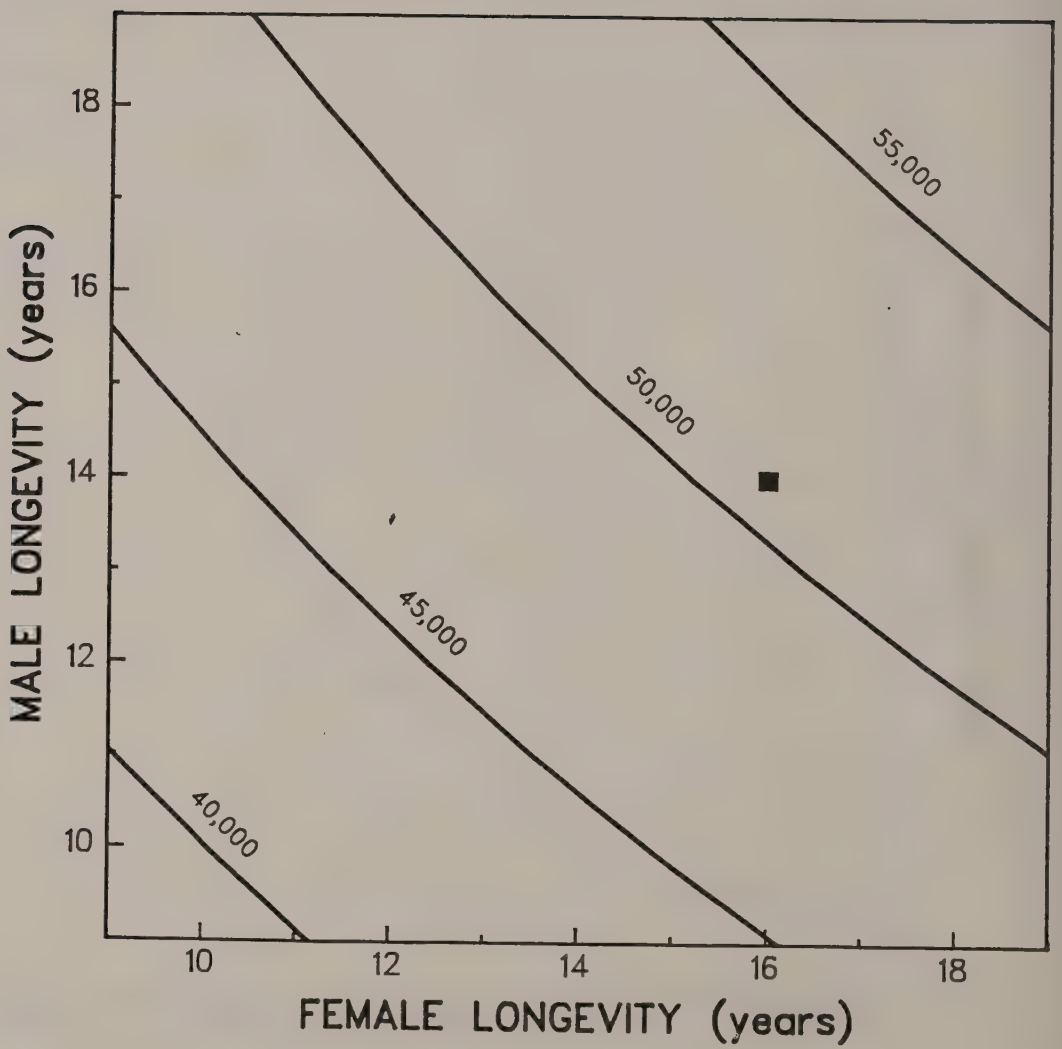

Figure 2. Contours of population estimates resulting from assumptions about male and female longevity (defined here as the 99th percentile of the age distribution). Sex-specific survivorship schedules for southern elephant seals (McCann 1985) were scaled to have longevities between 9 and 19 years. The solid square represents the estimate assumed to be most likely (50,800).

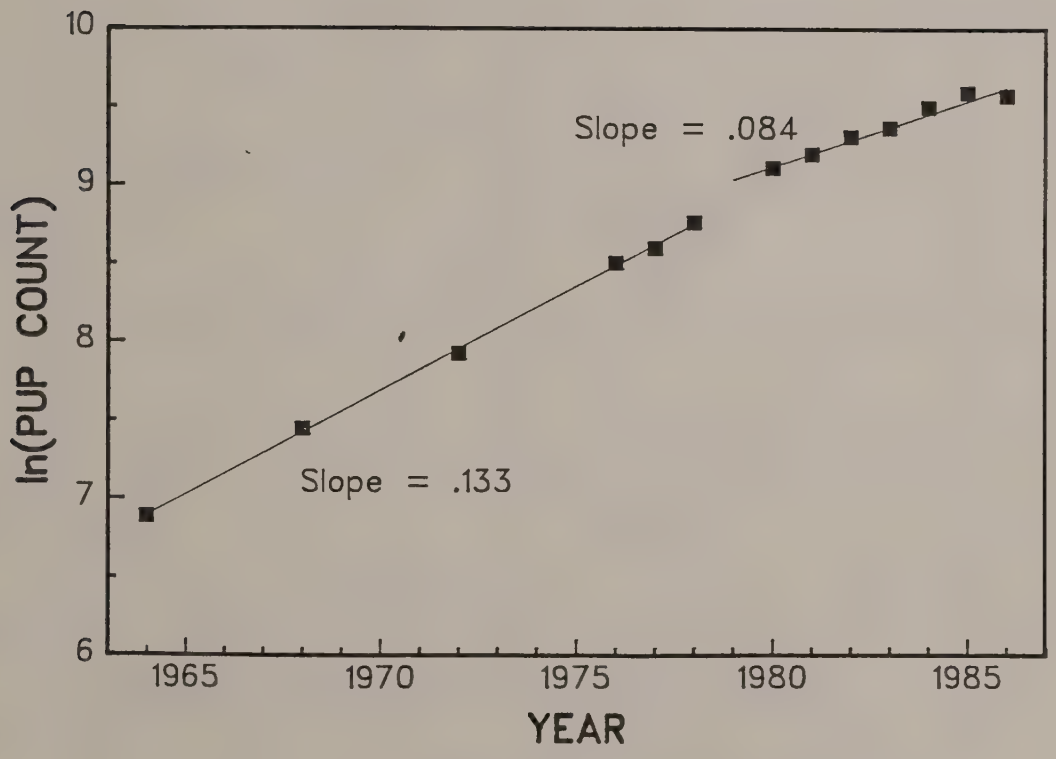

Figure 3. Natural logarithm of pup counts plotted against year, showing regression lines and slopes for the periods 1964 through 1978 and 1980 through 1986.

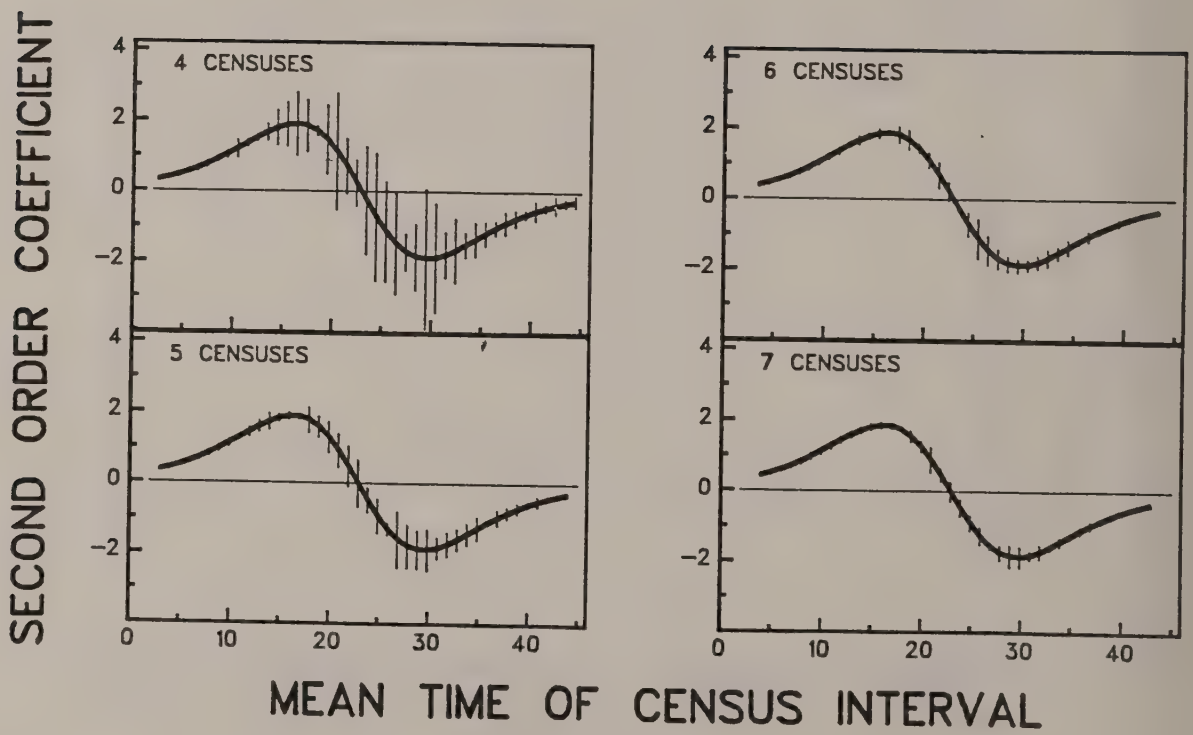

Figure 4. Second order regression coefficients computed from a hypothetical logistic population trajectory using intervals of from 4 to 7 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are ± 2 standard errors of the coefficients.

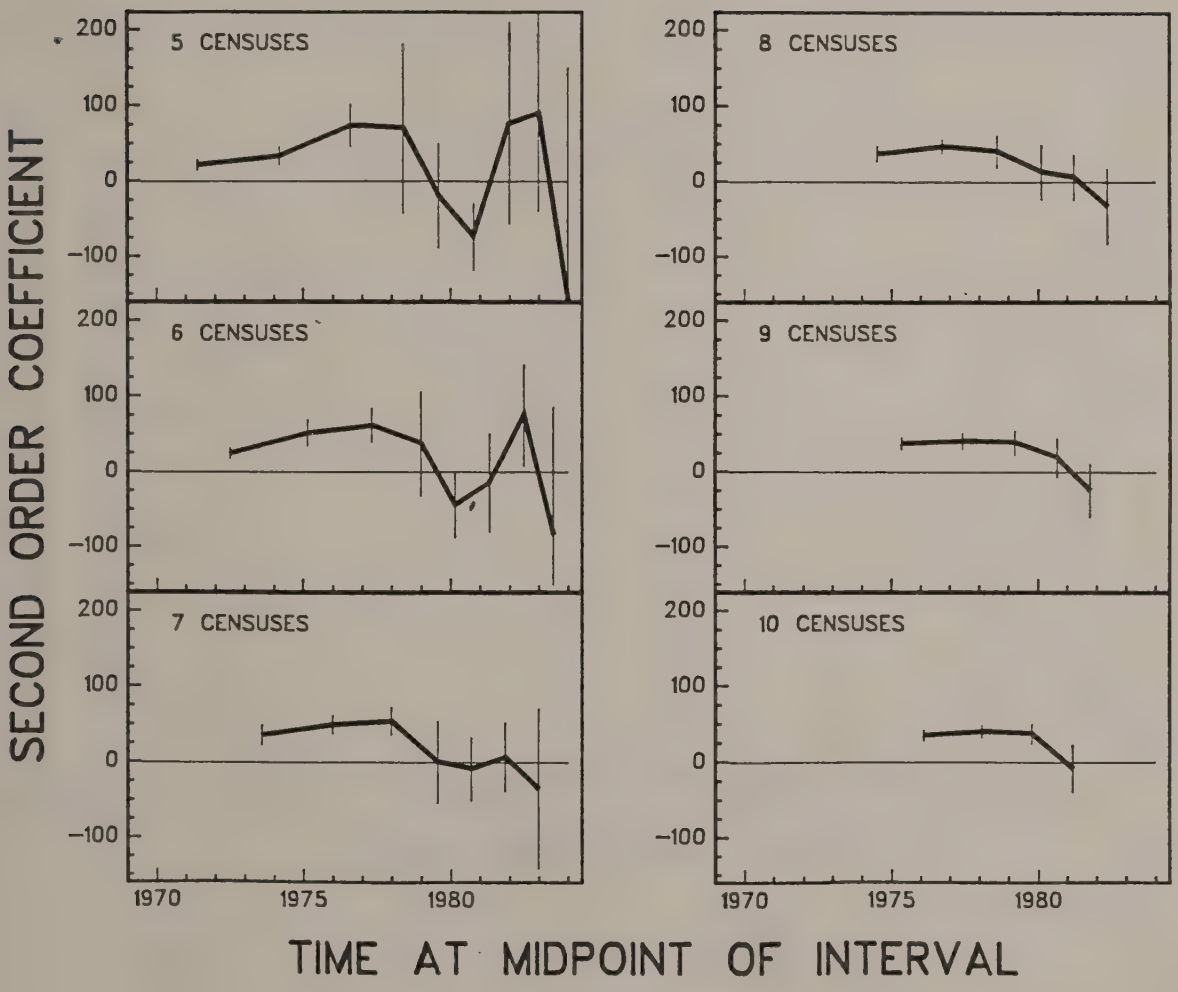

Figure 5. Second order regression coefficients computed from the trajectory of total pup counts in Figure 1. Regressions were computed for intervals ranging in size from 5 to 10 censuses. The intervals were moved along the trajectory in steps, computing a new regression at each step. Error bars are $\pm$ 2 standard errors of the coefficients.

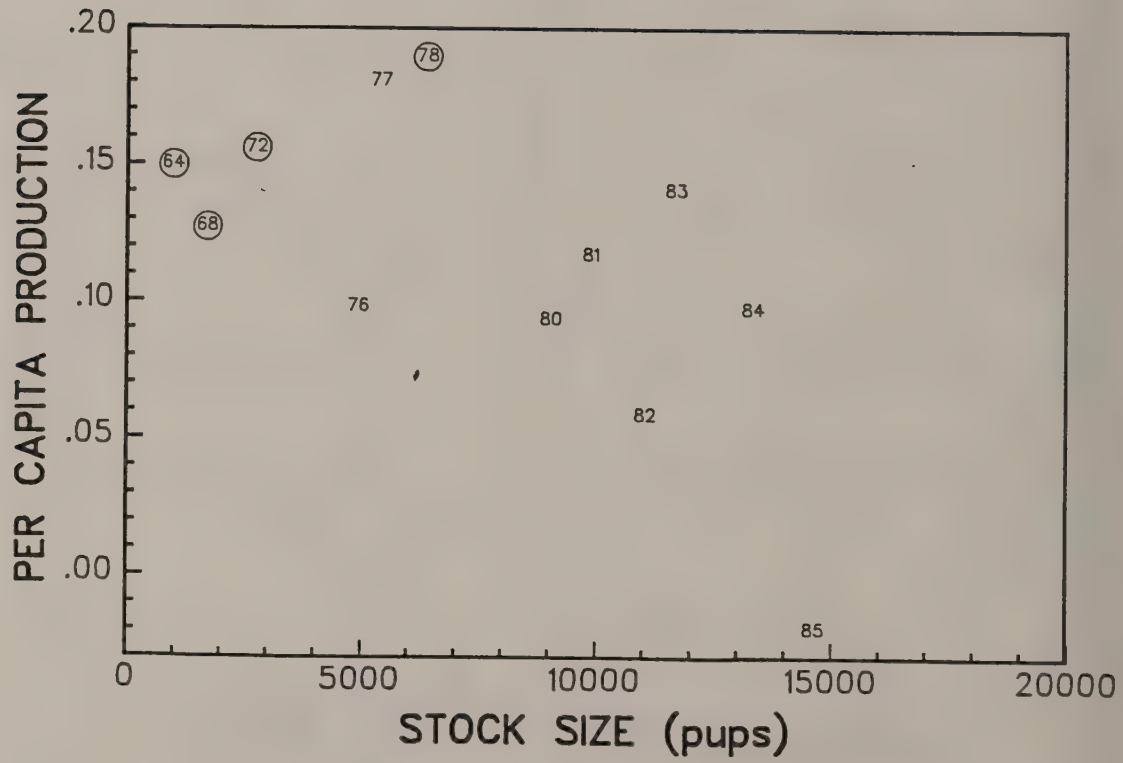

Figure 6. Estimates of per-capita production plotted against stock size (pups). Per-capita production was estimated as the first difference of the pup count time series, divided by the associated pup counts. Symbols are years. Per-capita production values for circled years were estimated as described in the text.

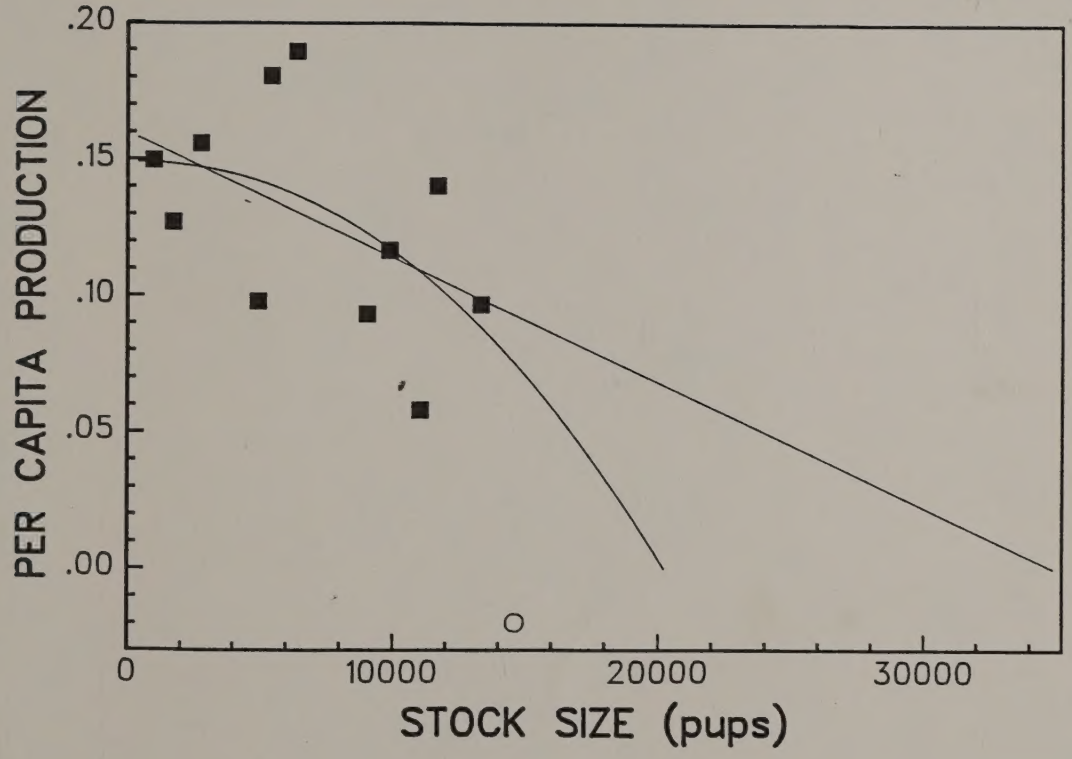

Figure 7. Estimates of per-capita production plotted with regression estimates of a nonlinear, 3 parameter production curve and a linear, 2 parameter (logistic) curve. The regressions were computed with the 1985 datum (open circle) excluded. Parameter estimates are given in the text.